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ON THE METHOD BY WHICH *STENUS* AND *DIANOUS*
(COLEOPTERA : STAPHYLINIDAE)
RETURN TO THE BANKS OF A POOL

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With 14 Text-figures

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I. INTRODUCTION

THE Steninae appear to be the only animals that move over water by lowering the surface tension behind them. The substance that lowers the surface tension is secreted by a pair of glands that open on either side of the anus. All Steninae appear to produce a similar substance but only some can use it for an astonishingly rapid movement over the water surface. This movement is here called "skimming".

There are seventy-one British species of the genus *Stenus* Latreille, and one of the genus *Dianous* Samouelle. Among the species of *Stenus* that frequently come into contact with water there appears to be an evolutionary sequence. Those that live in relatively marshy places first attempt to walk on the surface of the water before secreting, and they also use their legs while skimming. On the other hand, many species that live on the banks of torrential streams do not attempt to walk on the water surface but secrete immediately on contact with water. These do not employ their legs while skimming but hold them in close to the body. The only British species of *Dianous*, *D. coerulescens* Gyll., behaves in this way. In addition to this, if any of these beetles are thrown into a pool they will not stay out on the water surface but will at once return to the bank.

In nearly all natural habitats the banks of a pool must be dark as compared with the sky, and many banks rise steeply from the water. It early appeared that when beetles moved towards such banks they might have reacted to the contrast afforded between the bank and the sky. Heberdey (1944) believed *Paederus* did this in its return movement. He also supposed that *Paederus* regained the bank by a negative phototaxis and thought that banks were selected only when they provided a contrast

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at a critical height above the water and a minimal horizontal extent. All this seems to have been based only on general observation. The present paper is an account of an experimental investigation of the return movement. Tests were first made in the laboratory in order to suggest how suitable field experiments might be devised.

In the laboratory experiments beetles walked or swam on the surface of water. Some of the species used ordinarily skim on water, e.g. *Stenus pubescens* Stephens. In such cases the anal gland secretion was temporarily exhausted before the test by making the beetle skim on water for several minutes. In this way the beetles could be kept on a small artificial water surface long enough for their behaviour to be observed. The only effect of this seems to be that the beetles are slowed down, because they can return directly to a bank whether or not they employ the anal gland substance. The behaviour recorded has been obtained repeatedly with six species of *Stenus*; *S. pallitarsis* Steph., *S. binotatus* Ljungh, *S. pubescens* Steph., *S. boops* Ljungh, *S. latifrons* Er., and *S. flavipes* Steph., and with *Dianous*. The accompanying table summarises the number of trials made in the experiments selected for description.

Nature of experiment	Result	Species used	Number of trials	Total number of track records
Laboratory demonstration of orientated movement	Fig. 1	<i>S. pallitarsis</i> <i>S. binotatus</i> <i>S. pubescens</i> <i>S. latifrons</i> <i>S. flavipes</i> <i>S. boops</i>	12 or more for each species	123
Preference for marginal contrast	Fig. 2	Ditto	6 or more for each sp.	50
	Fig. 3	"	Ditto	50
	Fig. 4	"	12 or more for each sp.	107
Influence of contrast and directional light	Fig. 8	"	6 or more for each sp.	53
	Fig. 9	"	12 or more for each sp., but most with <i>S. pubescens</i>	96
Movement away from a bank	Fig. 11	"	12 or more for each sp.	83
	Fig. 12	"	Ditto	110
Orientation to part of a bank	Fig. 13	"	6 or more for each sp., but most with <i>S. pubescens</i>	54
Orientation with and against a current	Fig. 14	"	Ditto	50

II. THE DEMONSTRATION OF ORIENTATED MOVEMENT IN THE LABORATORY

The apparatus used in the first series of experiments consisted of a circular metal trough, twenty inches in diameter and four inches deep. The entire inner surface of the trough was painted black and in all experiments it was filled with water to a depth of two inches. A 60-watt lamp, one and a half feet above the water surface, was always lit. Beetles were dropped on to the water and presented with various black figures painted on the inner surface of a white paper cylinder which could be rotated about the trough. Alternatively, differently painted cards were clipped to the edge of the trough and its black wall covered with white paper. The effect of

this was that only the cards set against the white paper cylinder could be seen from the water surface. Four experimental arrangements can be seen in the cut-away drawings given with figures 1-4. When needed, a steady slow current could be set up in the water and the paper cylinder was turned by hand or by using a small electric motor.

When beetles moved towards presented figures, orientation was demonstrated only if they made a movement to compensate for rotation of the paper cylinder. When beetles persisted in swimming towards the figures the cylinder could be turned steadily and beetles made to cross and recross the water surface.

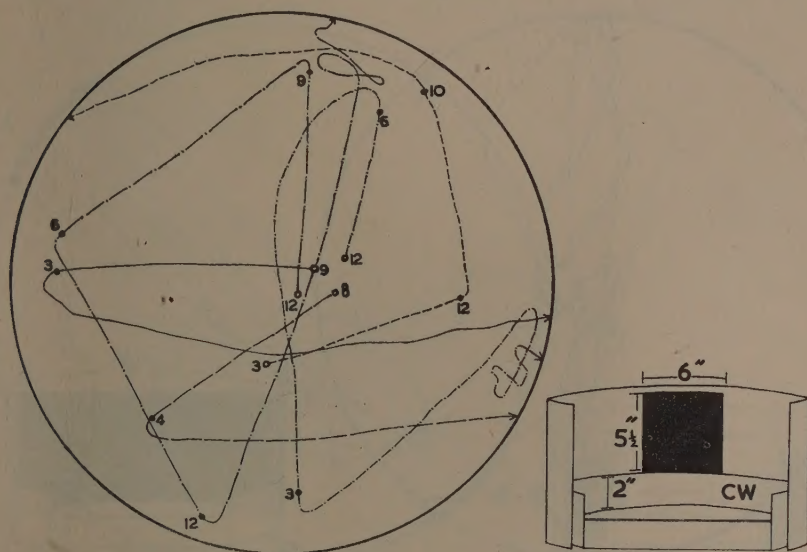


FIG. 1.—Reaction of *Stenus pallitarsis* Steph. in an experiment designed to test the compensation to movement of a rectangle above the covered inner wall (CW) of a circular trough. Result diagram conventions and other description in text. Cut-away drawing shows experimental conditions.

In the experiment, illustrated in figure 1, the wall of the trough was covered with white paper. A black rectangle was painted on the inner surface of the paper cylinder so that the situation presented to a beetle dropped on to the water was that shown in the cut-away figure. The paths taken by five beetles are shown. The point at which the beetle was put on the water surface is shown by a small circle. The figure placed by the circle indicates, as with a twelve-hour clock, the direction of the centre of the rectangle during the first part of the beetle's course. Where a dot interrupts the track, this indicates the point at which the paper cylinder was rotated, and the position of the rectangle after such movement is shown by a clock number against the point of movement.

A comparison of the paths with the clock numbers along them shows how the beetles persisted in swimming to the rectangle. In following the moving rectangle beetles turned with the direction of rotation and not against it. Two beetles circled a little way from the wall before landing, although all of them swam directly towards the rectangle from points across the trough. The tracks shown are for *S. pallitarsis* Steph., but all the other species of *Stenus* tested behaved similarly.

Control experiments showed that beetles had no preferred direction of movement within the trough, neither did they respond to movement of the paper cylinder

without movement of a rectangle. It may be noted that when a black paper rectangle was clipped over the paper-covered wall of the trough so that it contrasted well with it and with the paper cylinder beyond, *i.e.* when the rectangle rose from the water surface itself, then beetles swimming to it never circled before landing. Conversely, orientation to rectangles painted on the paper cylinder was poor if the black wall of the trough was exposed. In such experiments beetles sometimes ignored movement of the rectangle, and this was most noticeable when beetles had swum to within three or four inches of the wall. The paper cylinder was never turned at a rate of more than 4.2 inches per second.

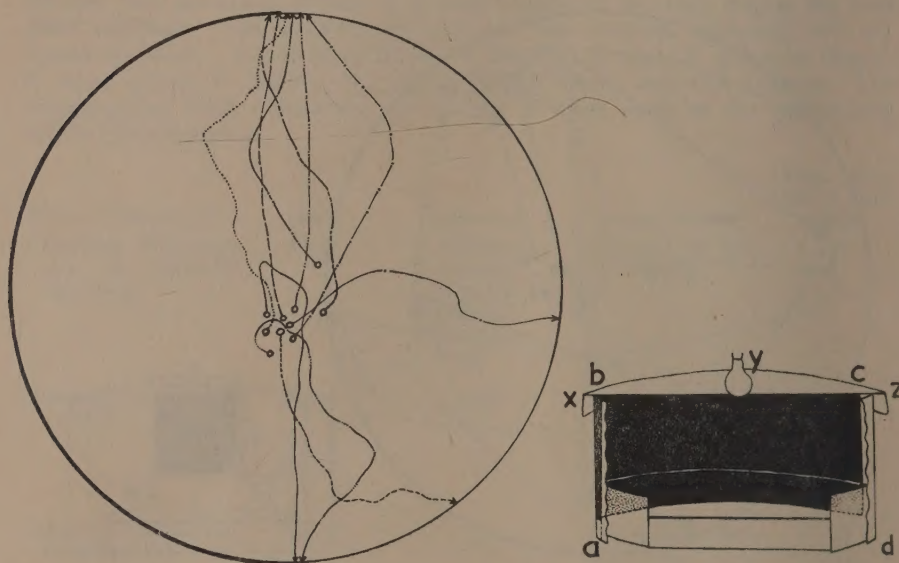


FIG. 2.—Reaction of *Stenus pallitarsis* Steph. in an experiment designed to test the influence of one border of a rectangle on the ability of beetles to make orientated movements. Cut-away drawing shows experimental conditions: the rectangle (*abcd*) occupies one-half of the circumference of the paper cylinder and extends to its top. Contrast between the upper border of this rectangle and the well-lit room is prevented by the close-fitting black paper screen (*xyz*). The rectangle occupies the left half of the result diagram.

III. FEATURES WHICH INFLUENCE ORIENTATION IN LABORATORY EXPERIMENTS

Beetles orientated very well to black rectangles which did not extend to the top of the white paper cylinder. They orientated equally well to those that did. In both cases beetles swam equally to the vertical edges and centres of the rectangles. Where rectangles were used that reached the top of the paper cylinder this behaviour suggested a test for any ability beetles might possess to select one edge of a rectangle.

In the experiment, a result of which is shown in figure 2, contrast between a rectangle extending to the top of the paper cylinder and the lights of the room was prevented by use of a black screen. The situation devised can be seen in the cut-away sketch. The ten tracks shown were obtained with *S. pallitarsis* Steph. The beetles swam mostly to the vertical edges of the rectangle and a few swam towards that half of the trough where the black metal wall provided a good contrast against the white paper cylinder. Once again, such movement could be eliminated by covering that half of the wall with a strip of white paper. Similar results were obtained with the other species of *Stenus* tested. It could be shown that beetles would swim to the vertical edges and avoid the centres of rectangles only ten inches

wide. Horizontal contrast at the top of the rectangles could easily be re-established by use of a broad strip of white paper. When the black overhead screen was then kept in position beetles did not show a preference for the vertical edges but swam equally to them and to the centres of the rectangles. This seems to show that when beetles moved to the vertical edges in the experiment illustrated, they really aimed for them and were not simply swimming beneath the margin of the black screen above them. The experiment establishes that beetles only swim to the centre of a wide rectangle when it affords a strong contrast at its upper horizontal edge.

Some experiments were made in which the wall of the trough was covered with white paper and two rectangles were set up opposite each other. When the rect-

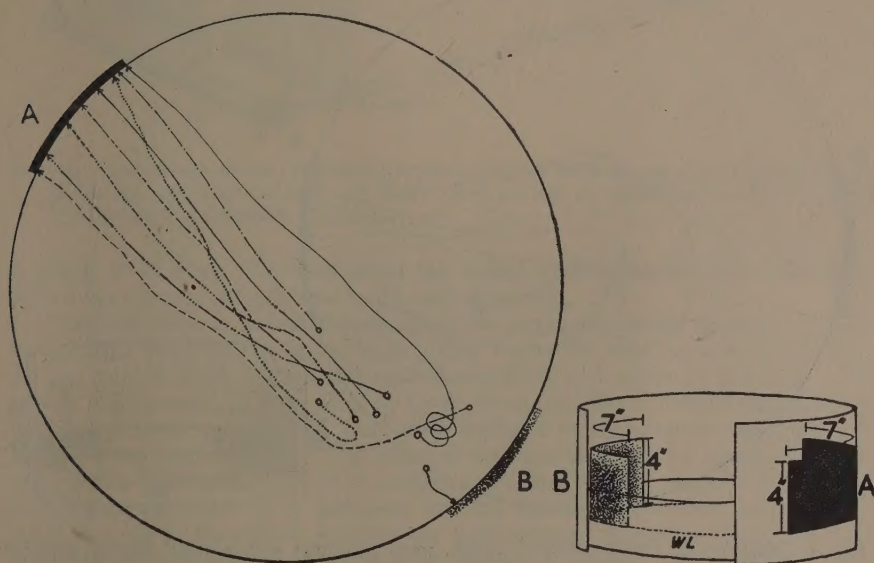


FIG. 3.—Reaction of *Stenus pallitarsis* Steph. in an experiment designed to test the influence of marginal contrast in determination of rectangle choice. Cut-away drawing shows experimental conditions. The heavily painted rectangle is at the left in the result diagram.

angles were of equal width the higher was preferred, and where the heights were equal the wider one was chosen by beetles put on the centre of the water surface. On the other hand, beetles did not select a rectangle eight inches wide and with a height of five inches measured from the water surface when this was set opposite one only four inches wide and seven inches high; they swam equally to both. It appeared that the beetles were indifferent to height, width and area of the rectangles used, but might select them for length of border above the water surface or something dependent on this.

All the rectangles used in the previous experiments were painted an intense black in such a way that their edges when seen against the white paper cylinder provided the strongest possible contrast. The amount of contrast will depend upon the length of border above the water surface which can be seen against the background, but the quality of contrast will depend on how the rectangle is painted.

Beetles were tested for preference between two rectangles offering different quality of contrast. In an experiment, a result for which is given as figure 3, beetles were presented with the situation shown in the cut-away drawing. The rectangles were of equal size. One was painted in the same way as before but the other,

rectangle *B*, had the paint thinned towards its edges so that they provided a relatively feeble contrast when viewed against the white paper cylinder. The black wall of the trough was covered with white paper except where the rectangles were clipped over it.

Beetles preferred the rectangle which provided stronger contrast. They could be dropped on to the water surface near rectangle *B*, but ignored it and swam right across the water surface to the other one. Sometimes beetles spiralled or wandered on the water surface between the rectangles but almost invariably chose the rect-

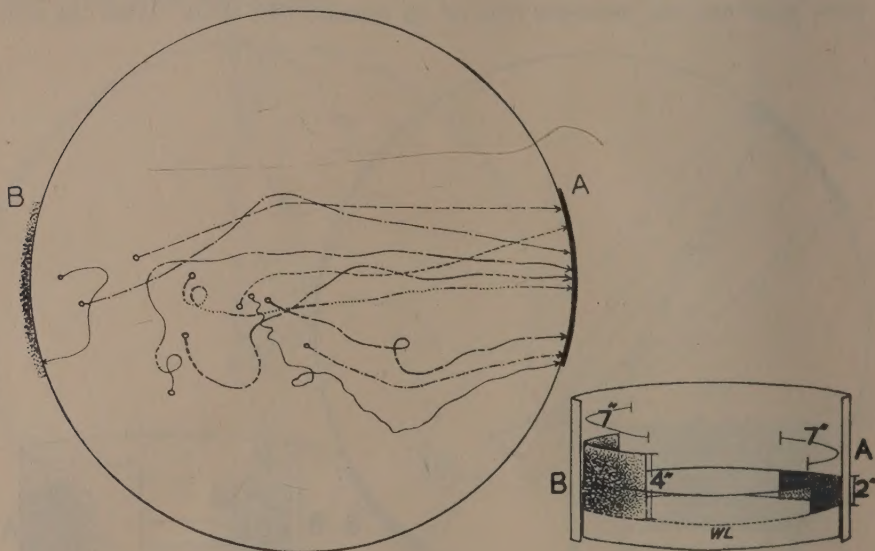


FIG. 4.—Reaction of *Stenus palliarsis* Steph. when presented with a small sharply bordered rectangle placed opposite a larger rectangle not affording strong marginal contrast with the paper cylinder. Cut-away drawing shows experimental conditions. The heavily painted small rectangle is shown at the right in the result diagram.

angle with heavily painted edges. Beetles always swam to the lightly painted rectangle when this was presented singly. As the result of the experiment illustrated in figure 4 shows, the beetles persisted in selection of a heavily painted rectangle when it was only half the size of the other in which paint was concentrated at the centre and thinned at the edges. The track records are all for *S. palliarsis* Steph., but the five other species of *Stenus* used also showed this behaviour.

These experiments prove that beetles of the genus *Stenus* can estimate the contrast set up at the edges of figures in the laboratory, and choose between them on this basis. Nothing in the experiments suggests that beetles which swim towards a figure can in any way estimate its nearness.

IV. MECHANISM OF THE ORIENTATED MOVEMENT

The criterion for orientated movement has been that beetles should swim persistently to the presented figures. Beetles estimate contrasts very well, and it seems most likely that when they moved towards a rectangle they really aimed for it. On the other hand, it is conceivable that they arrived at the rectangles by an orientation movement away from the unpainted parts of the white paper cylinder. To see

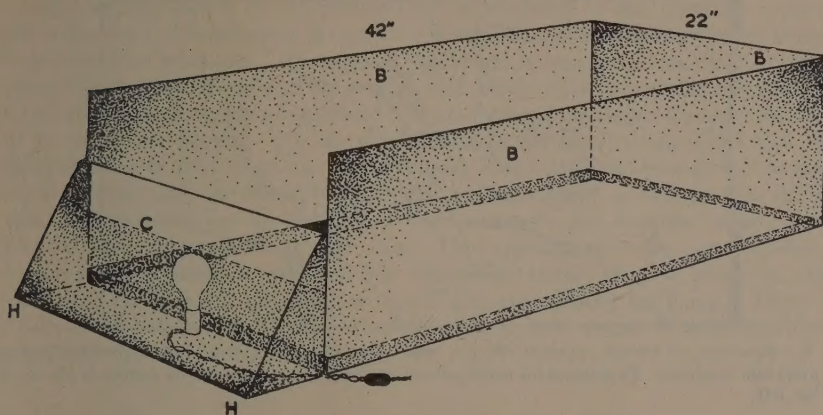
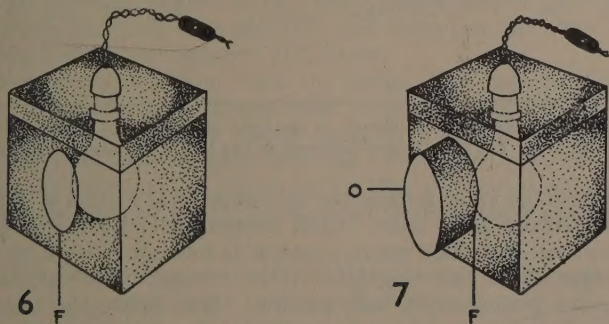


FIG. 5.—Arrangement for an experiment in which a strong contrast was produced immediately before the only source of light. (B, black velvet screens; C, painted card; H, black paper hood preventing dispersion of light.)

if this is at all likely, the reactions of the beetles were determined when presented with a light source and contrast in the same direction.

This was done in an experiment using the apparatus shown in figure 5. The trough used was forty-two inches long, twenty-two inches wide, and two inches deep. It was painted black on its inner surface and filled with water to the brim. The trough was screened on three sides by black velvet, and the only light came from an enclosed 100-watt lamp placed four inches behind a paper rectangle, the lower half of which was painted black. The effect of this was to provide a strong horizontal contrast six inches above the water surface and before the only source of light. The experiment was made in a darkroom and the beetles' movements were watched through a slit in the velvet opposite the light source. Since the beetle has been shown to move at one and the same time towards a contrast and towards a light source (*i.e.*, up a gradient of light intensity), it cannot arrive at the black rectangle by movement away from the brighter (unpainted) areas.

All species of *Stenus* tested moved towards the contrast provided and against the light direction. Similar results were obtained with or without water filters before the light, and for light intensities between 0.6 and 19 foot-candles as determined at the water surface one foot from the lamp.



FIGS. 6-7.—(6) The device placed behind a sheet of tracing paper to give the diffuse light source described in the text. (7) The same device modified to give light with clear marginal contrast. (F, eight filter papers; O, one thickness of tracing paper.)

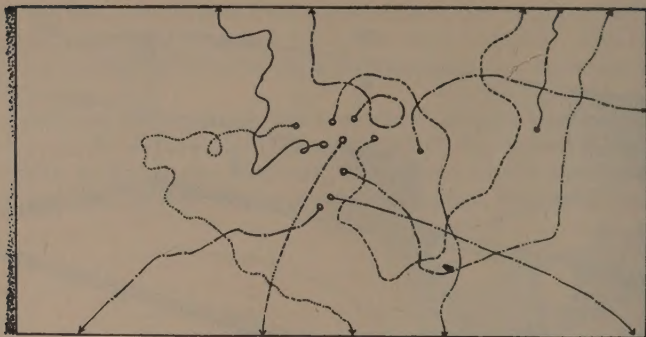


FIG. 8.—Reaction of *Stenus pubescens* Steph. when presented with a light source not affording marginal contrast. Experimental arrangement in text. The diffuse light source is shown to the left.

In all previous experiments light and contrasts about the edges of figures have been presented together, but it is easy, by using sufficiently weak lights, to separate these two features. This was done in an experiment for which the device shown in figure 6 was made. The lamp was enclosed in a tin box which had been painted black. The amount of light escaping could be cut down by fixing filter papers over the hole which was two inches across. When a 60-watt bulb was used and eight thicknesses of filter paper were stuck over the hole, the intensity of illumination at the water surface was one foot-candle. To provide the light source a piece of tracing paper twenty-two inches wide and eighteen inches high was held vertically at one end of the trough. The device described was placed behind its centre so that the filter papers were an inch from the tracing paper surface. Black velvet screens bordered the remaining three sides, and the experiment of putting beetles on to the middle of the water surface was done in a dark room.

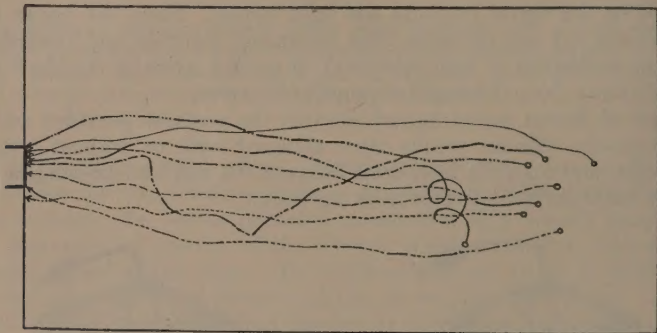


FIG. 9.—Reaction of *Stenus pubescens* Steph. to the light source shown in fig. 7. Experimental arrangement in text. The light source is shown to the left of the result diagram.

When seen from the water surface, the light source was a patch of diffuse light at the centre of the tracing paper sheet. Light intensity fell off in such a way towards the edges of the sheet that there was no appreciable contrast between its borders and the vertical edges of the two long black velvet screens. None of the species of *Stenus* tested swam persistently to such a source. Most frequently, beetles spiralled about on the water surface and went equally to all points about the trough. A result for a test in which ten individuals of *S. pubescens* Steph. were used is given as figure 8.

The light intensity of the diffuse light source used in the previous experiment was very low. Nevertheless, it could be shown that lack of orientation to it did not result from its weakness. Thus, when the boxed-in lamp was modified, as shown in figure 7, and set at one end of the trough with black velvet everywhere else about the edge, beetles persistently swam to it. Figure 9 shows the tracks for eight individuals of *S. pubescens* Steph. The obvious difference between the modified and diffuse light sources is that only the former allows clear marginal contrast between the tracing paper and the black velvet. The beetles reacted as though this difference was the significant one for them, and they swam to the modified source when a 25-watt lamp replaced the 60-watt one. This experiment is the most difficult one to carry out, because in order to see where the beetle goes, it must be kept in view against the small and weak circle of light provided by the lamp. There is no difficulty in watching the beetles when the diffuse light source is used provided the observer's eye is at water level.

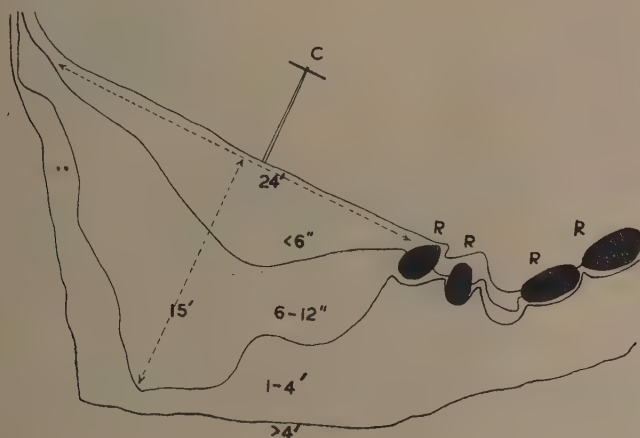


FIG. 10.—Plan of a low-lying bank off which painted cards were suspended in the position indicated by *C*. Contour lines are drawn at six inches, twelve inches, and four feet. (*R*, clump of rushes.)

Finally, a number of experiments were made using unilaterally blinded beetles. Whitehead's varnish was painted on to the eye and covered with indian ink. Beetles treated in this way and released on to a well-lit water surface showed no tendency to spiral towards the blind side, although such behaviour has often been reported for insects which show clear negative phototaxes.

These experiments show that when the beetles swim towards a source of light they respond to the contrasts afforded about its edges. This makes it seem unlikely that in the earlier experiments beetles could have arrived at the rectangles by balancing away from light reflected from the white paper cylinder. When beetles swim towards the figures used in the laboratory they show a true orientation to them, and the feature selected by the beetles to direct the movement is marginal contrast.

V. CONDITIONS UNDER WHICH BEETLES CAN BE MADE TO SWIM AWAY FROM THE BANK OF A POOL

The results of the laboratory experiments suggested the design of field tests in which beetles were offered a choice between painted cards and the bank of a pool. It was found that, although beetles always swam to the bank where it was steep,

they could be made to swim away from the central part of the bank shown in figure 10. It can be seen that at this point the bank shelves gently into the water. Beetles thrown out on to the water surface opposite the mid-point of the bank ordinarily return directly to the edge; they do not swim to the steeper part of the bank about ten feet to the observer's right.

The cards used in the experiments measured twenty-two by sixteen inches, and were suspended from the end of a metal rod eight feet long so that the lower border dipped into the water. The appearance of the experimental arrangement to an observer is shown in figure 11, and the device has been included in plan view in figure 10. These experiments were done only on sunny and completely calm days.

When a black painted card was used, beetles swam to it and ignored the bank

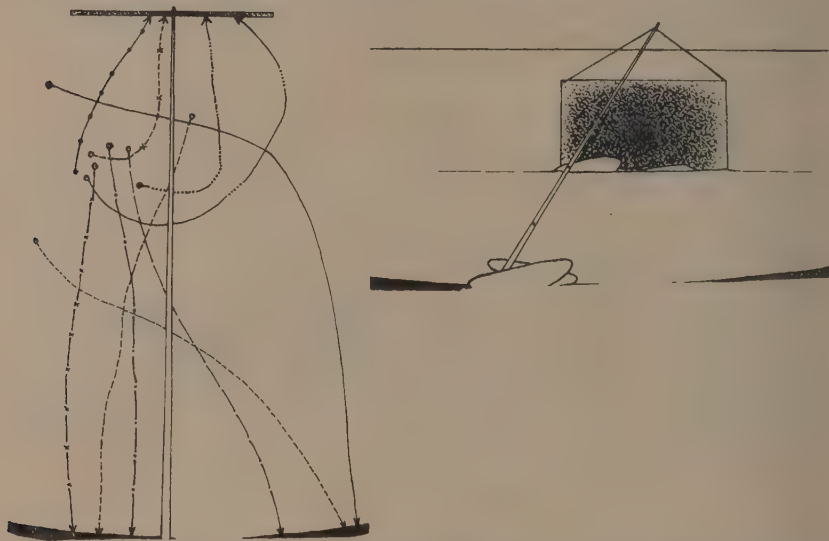


FIG. 11.—Reaction of *Stenus pubescens* Steph. when dropped between the card shown in the right hand drawing and the mid-point of the low-lying bank of a pool shown in figure 10.

when released half-way between the two. On the other hand, when a card painted as in figure 11 was used, beetles swam equally to the bank and card, and some beetles ignored the card when put onto the water only two feet from it. The tracks shown in figure 11 are for *S. pubescens* Steph. The most remarkable result was obtained using the card shown in figure 12. In this case one edge has been heavily painted and paint thinned out towards the other. Beetles which were started half-way between the card and the mid-point of the bank almost always swam to the card and preferred the heavily painted edge. The tracks shown in figure 11 are for seven individuals of *S. pubescens* Steph., a beetle common about the margins of many ponds. Similar results were obtained with the other species of *Stenus* tested.

It must at first seem unlikely that the bank of a pool should offer contrast against the sky comparable with that set up at the edges of painted rectangles in the laboratory. Nevertheless, inability to characterise all the information which the bank of a pool might afford to returning beetles did not prevent design of experiments in which they were "tricked" into swimming away from it. Beetles were most successfully tricked by cards which afforded strong contrast between their heavily painted edges and the sky. This could happen if the card had elicited a reaction which would

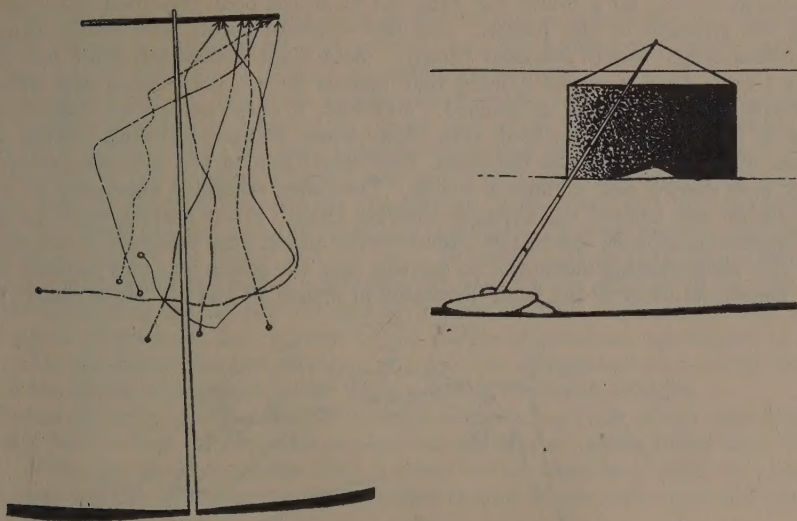


FIG. 12.—Reaction of *Stenus pubescens* Steph. when dropped between the card shown in the right hand drawing and the mid-point of the bank of a pool shown in figure 10.

ordinarily guide the beetle directly to the bank. In their return movement beetles aim at the contrast established between the bank and the sky.

VI. ORIENTATION TO PARTS OF A BANK

In a number of cases beetles swimming to the bank of a pool behaved as though they had aimed for clumps of rushes growing at the water's edge. Such behaviour is illustrated in figure 13, and was seen when a breeze blowing parallel to the bank carried returning beetles laterally from a position opposite large clumps of rushes to a position opposite a low-lying part of the bank with no rushes. Behaviour

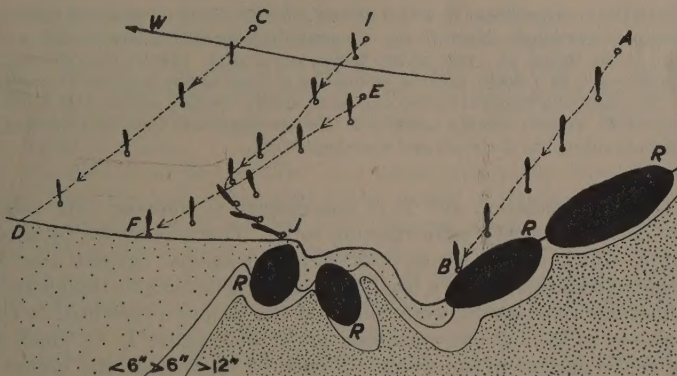


FIG. 13.—Diagram showing the way in which beetles compensated to their carriage past clumps of rushes. The bank shown is at the right hand of figure 10. (A-B and C-D, paths of beetles released near the high and low parts of the bank, respectively; E-F, frequently recorded return path of smaller swimming species of *Stenus*; I-J, paths recorded for *S. pubescens* Steph. and *S. binotatus* Ljungh and by other skimming species. R, clump of rushes; W, direction of breeze.)

depended on how far a beetle was flung out on to the pool, the speed of its return, and the strength of the breeze. The best demonstrations were made using *S. pubescens* Steph. and *S. binotatus* Ljungh. Both these beetles can skim, but when they secrete they move so quickly that breezes do not carry them any distance laterally before the bank is reached. However, if these beetles are thrown only four or five feet from the bank they often return without secreting. When they swam under the conditions indicated, they sometimes turned into the current as they were carried past clumps of rushes. They then struggled vigorously to reach the rushes and ignored the adjacent shelving bank. If the current made progress by swimming difficult, the beetles often secreted and at once skimmed to the rushes.

This compensating movement to carriage past the rushes was only noticed when the beetles returned to the bank illustrated in figures 10 and 13. It is clearly trig-

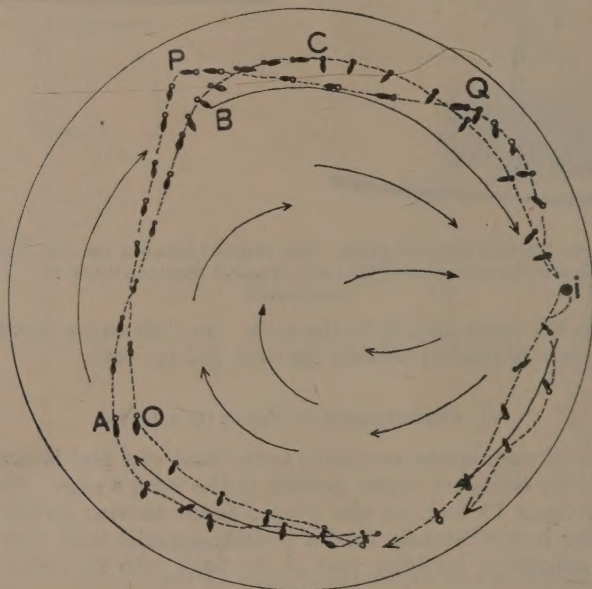


FIG. 14.—Result of an experiment in which *Stenus pubescens* Steph. was tested for orientation to the black paper rectangle shown in the cut-away drawing with figure 1, while a current ran clockwise in the trough at a rate of two inches per second. Beetles were dropped on to the water surface at *i*, (3 o'clock), and the inclination of their bodies is shown at points along the tracks. The head of a beetle is shown as a small circle. During course *A-B-C*, the rectangle was kept at 11 o'clock; during track *O-P*, the rectangle was held at 11 o'clock; at *P* it was suddenly rotated to 2 o'clock and then kept there.

gered by optical stimulation and it is unnecessary to suppose that when beetles turned into the current they were reacting to it. This was shown by a laboratory experiment in which beetles swam both with and against current direction when compensating to displacement of a black rectangle. The circular trough and rotating paper cylinder described earlier were used, and the situation presented to the beetles was that shown in the cut-away drawing given with figure 1. A small air-pump provided a gentle current in the water. Figure 14 shows that the beetles will not swim into a current unless by doing so they move towards the black rectangle used.

If the black inner wall of the trough was exposed it was more difficult to make beetles swim with the current to follow the moving rectangle than to make them swim against the current. This was due to the difficulty in turning the paper cylinder at the correct rate. Where current direction and rectangle movement are both

clockwise, too slow a rotation of the rectangle did not induce change of body direction, whereas too quick a movement was ignored, and the beetles were again carried passively by the current to a position opposite the rectangle.

It is interesting to note that beetles which make compensating movements before clumps of rushes do so although the far part of the low-lying bank, shown in figure 10, is just as high as the bank immediately behind the rushes. If we consider the geometry of the situation afforded to a beetle as it nears the clumps of rushes, we see that the contrast between the distant part of the bank and the sky would appear at a lower angular elevation than any contrast established between the bank immediately behind the rushes and the sky. It seems unlikely that beetles which switch course towards the rushes can distinguish between the nearness of the rushes and the distance of the far part of the shelving bank. High angular elevation is a good signal of nearness, but, in view of the results of previous experiments, it is likely that the higher angular elevation and increase in apparent size of the bank behind the rushes is preferred for the better contrast conditions afforded.

Beetles do not pay any attention to single reeds during their return movement, and only land on them if they swim so near that capillary attraction forces come into play. When the beetles swim the body is flexed so that mounds of water are raised at its ends and this use of surface forces enables them to climb easily on to the reeds.

VII. ORIENTATED MOVEMENT IN *Dianous*

Laboratory and field tests were made with *Dianous coerulescens* Gyll. The beetles of the genus *Stenus* which have been tested in the previous experiments were collected from the edges of large pools. *Dianous* is not found about the edges of these pools but is common along quick-flowing streams. It prefers moss-covered places at the sides of water-falls or stones in mid-stream. Unlike some species of *Stenus*, *Dianous* always secretes immediately when thrown on to a water surface. If *Dianous* is thrown out on to the surface of a pool, it secretes and often skims towards the centre, but where the pool is large, it always turns suddenly and skims directly to the near bank.

Dianous showed no tendency to skim towards cards, however painted, when these were suspended off a bank. *Dianous* compensated to rotation of black rectangles about a water-filled trough, but the beetles often landed to one side of the rectangle and compensation to movement of the figure was not as precise as that shown in comparable experiments by species of *Stenus*. In the laboratory the beetles walked over the water surface after their anal gland secretion had been exhausted. This enabled tests to be made with apparatus of reasonable size, and trials showed that under calm conditions *Dianous* can swim or walk over the water surface directly back to the banks of a pool.

Dianous spiralled towards the blind side when unilaterally blinded, and went directly away from the light sources to which species of *Stenus* showed a positive reaction. This, together with the fact that *Dianous* never skims away from the observer and right across a large pool, suggests that it might return to the bank by simply moving away from the greater amount of light at the centre of the pool. The plentiful and immediate secretion put out by the anal glands when *Dianous* is dropped on to water could make this an effective method of return.

A consideration of the habitats of *Stenus* and *Dianous* may account for the apparent neglect of contrast information by *Dianous* and its use by *Stenus*. *Dianous*, unlike the six species of *Stenus* used throughout this work, is found in mid-stream or water-fall habitats and not about the margins of large pools. In the latter habitat the bank provides a contrast when viewed against the sky. Localised contrast of this sort could not be provided by the steep banks of the torrential streams preferred by *Dianous*. Directional light could, at most, serve to indicate the difference between

"along" and "across" the stream, but it is most unlikely that *Dianous* normally responds to a feature of this sort; It need not; when *Dianous* is displaced from a stone in a fast flowing stream it secretes instantly and skims to another stone or to the bank almost at once whatever its direction of movement.

Observation suggests that beetles of both genera are active by day and not by night. Only active beetles could wander out on to the surface of a pond, and, presumably, they would be more easily blown out on to it than beetles hidden deep among the rushes. The contrast of the bank against the sky is strong in the day-time, whereas on many clouded nights it would be very poor.

VIII. SUMMARY

Laboratory experiments with beetles of the genus *Stenus* showed that the direction of their movement over a water surface could be controlled by varying the quality and amount of contrast information offered. *Dianous* persistently moved away from light sources and acted as though ignoring contrast information. Field experiments confirmed the conclusions drawn from the results of laboratory tests.

It appears that *Stenus* returns to the bank of a pool by orientating towards the contrast established between the edge of the bank and the sky. *Dianous* may skim to the near bank of a suitably large pool by means of a simple negative reaction to light. These different ways of using information can be related to the presence of strong localised contrast in the habitat of pond dwelling species of *Stenus* and its absence in the habitat of *Dianous*.

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X. REFERENCE

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